

EFFECTS OF NUTRIENT ENRICHMENT AND GRAZING ON PERIPHYTON ASSEMBLAGES IN SOME SPRING-FED, SOUTH ISLAND STREAMS

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ABSTRACT

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The effects of nutrient enrichment and grazing on periphyton structure and biomass were investigated experimentally in spring-fed streams of inland Canterbury, South Island, New Zealand. After 2, 4 and 6 weeks, algal biomass on nutrient diffusion substrata (nitrogen plus phosphorus) was greater than on no-nutrient controls at all six sites, and was higher in grassland than beech forest streams. Colonising algae were mainly diatoms; species of *Diatoma*, *Fragilaria* and *Cymbella* dominating at open sites, and species of *Achnanthes*, *Cocconeis* and *Gomphonema* at forested sites. Exclusion and enclosure experiments at two springs demonstrated that natural densities of grazing invertebrates, principally the gastropod *Potamopyrgus antipodarum*, depressed algal biomass and modified assemblage structure. In particular, the filamentous diatoms *Fragilaria* and *Diatoma* were more abundant on substrata from which snails were excluded.

KEYWORDS: periphyton - epilithon - streams - nutrient limitation - grazing - *Potamopyrgus*.

INTRODUCTION

The composition, biomass and growth of epilithic periphyton in running waters are influenced by a number of environmental factors. Biggs (1988) identified the nature of the discharge regime, current velocity, and the size and stability of bed materials as of primary importance, and Rounick & Gregory (1981) noted that water temperature, light and nutrient availability, physical abrasion and grazing were other important variables that varied both seasonally and between streams.

The few investigations of periphyton communities made in New Zealand have been primarily taxonomic or concerned with water quality (Biggs 1985a). Several recent studies have examined the relationship between environmental factors and the development of nuisance growths of algae in rivers (Biggs 1985b, 1988; Biggs & Price 1987) and for using periphyton as a biological monitor of

water quality (Biggs 1985a, 1988). However, few ecological studies have considered small, nutrient-poor streams. Exceptions are some experimental studies of epilithon development, structure and function by Rounick & Winterbourn (1983) and recent investigations of stone-surface community dynamics in flood-prone, South Westland streams (Winterbourn *et al.* 1988; Graesser 1989). In the Westland streams, low standing crops of epilithic algae appear to be maintained primarily by physical factors (abrasion) although field experiments with nutrient-diffusing substrata showed that algal populations could also be nutrient limited (Winterbourn *et al.* 1988). A subsequent study in a small stream at Cass, inland Canterbury, demonstrated clearly that the growth of periphyton was nutrient limited in both forested and grassland reaches, and suggested that invertebrate grazers had a minor impact on epilithic biomass (Winterbourn in press). In contrast, Graesser (1989) found that the biomass of epilithon on tiles after 2 months in a west coast stream was on average 3.6 times greater when many grazing insect larvae were excluded.

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Although both nutrient limitation and grazing pressure have been identified as important factors that can affect epilithic algal biomass and growth in New Zealand streams, their relative importance has not been investigated at any one site. The present study had two main objectives. First, to investigate nutrient limitation of epilithic algal growth in 6 spring-fed streams in the Porters Pass-Cass region of inland Canterbury, and second, to examine whether grazing invertebrates affected periphyton biomass and composition at two of the sites where field experiments could be carried out readily and conspicuous populations of grazers were present.

STUDY AREA

Field experiments were conducted at 6 stream sites between Porters Pass and Cass in the South Island of New Zealand. Three sites were within mountain beech forest (*Nothofagus solandri* var. *cliffortioides*) and had moderately dense canopy cover, whereas the others were on unshaded, tussock grassland streams. Two of the latter were very close to their spring sources and had almost constant water temperatures. The catchments of all streams are used periodically for the grazing of cattle and sheep, but no stock were present during the course of the present study. Stream bed materials were predominantly cobbles and coarse gravels, although leaf litter, logs and branches were common in the forested channels. At the two springs aquatic macrophytes were present, the most common being *Nasturtium officinale* (Cass

Spring) and *Myriophyllum* sp. (Slip Spring).

On the three occasions that water samples were obtained from the study sites, concentrations of nitrate-nitrogen ($\text{NO}_3\text{-N}$) were always $<0.05 \text{ g.m}^{-3}$ and those of reactive phosphorus ($\text{PO}_4\text{-P}$) were below the detectable limit of 0.004 g.m^{-3} . They were therefore comparable to the mean nutrient values reported by Biggs & Close (in press) ($\text{NO}_3\text{-N}$, 0.053 g.m^{-3} ; $\text{PO}_4\text{-P}$, 0.0025 g.m^{-3}) for the alpine-fed Waimakariri River in whose catchment the present study sites lie. Other physical characteristics of the six sites are summarized in Table 1. Water temperature was almost identical at each site on each sampling day, and average current speed was similar at five of the six sites (twice as fast at Slip Stream). However, illuminance measured immediately above the stream bed between 1100 and 1400 h (N.Z. Summer Time) was substantially higher at the grassland sites (Table 1).

METHODS

NUTRIENT LIMITATION BIOASSAYS

Potential nutrient-limitation of algal growth was examined using nutrient diffusing substrata described by Winterbourn (in press) and Winterbourn *et al.* (1988). Individual substrates consisted of plastic cups (60 ml, surface area 12.6 cm^2) filled with 2% agar-nutrient solutions (see Table 2). Plankton netting ($100 \mu\text{m}$ mesh) secured tightly over the agar surface by a snap-on, plastic ring formed the colonization surface through which nutrients diffused. Sets of 10 cups were

Site (informal names)	Map reference (NZMS 1)	Width (m)	Current (cm.s^{-1})	Light (lux)	Temperature range ($^{\circ}\text{C}$)
GRASSLAND SITES					
Slip Spring	S74 164895	1	17	8560	8.5 - 9.0
Slip Stream	S66 182906	3	34	9655	9.0 - 10.0
Cass Spring	S66 229177	2	13	8010	9.0
FOREST SITES					
Middle Bush Stream	S66 236171	1	16	266	7.5 - 10.0
Steep Bush Stream	S66 237171	1	15	213	8.0 - 10.5
Reservoir Bush Stream	S66 235173	1	16	21	8.5 - 11.0

Table 1. Locations and physical characteristics of the 6 stream sites in the Porters Pass - Cass area. Stream width, current velocity, and illuminance are means from 3 or 4 sampling days. Temperature is the range recorded during field experiments.

Dates	Treatments	Sites
NUTRIENT ENRICHMENT EXPERIMENT		
8 March - 18 April, 1988	(a) No-nutrient controls	All sites
	(b) 0.66M NaNO ₃ + 0.06M KH ₂ PO ₄	All sites
NUTRIENT-GRAZER INTERACTION EXPERIMENTS		
(i) 3 September - 7 October, 1986	(a) No-nutrient controls	Cass Spring
(ii) 23 October - 28 November, 1986	(b) 0.33M NaNO ₃	Cass Spring
(iii) 28 August - 27 September, 1987	(c) 0.51M KH ₂ PO ₄	Cass Spring
	(d) 0.33M NaNO ₃ + 0.03M KH ₂ PO ₄	Cass Spring

Table 2. Dates, treatments and sites of the nutrient-enrichment and nutrient-grazer interaction experiments undertaken with different substrata.

pressed tightly into alternate cells of square plastic trays (modular floor gradings, 0.1 m²) and anchored to the stream beds with heavy stones placed along the sides of the trays so as not to obstruct natural flow patterns. Three trays, each containing five control (no nutrient) and five nutrient-added substrata arranged in an alternating pattern were placed at each of the six sites on 8 March 1988. One tray was collected from each site after 2, 4 and 6 weeks.

In the laboratory, the plankton netting was removed from diffusion substrata and soaked in 5 ml of 90% acetone (24 h, 5°C) to extract photosynthetic pigments. Concentrations of chlorophyll *a* and phaeophytin *a* were estimated by the method of Moss (1967a,b) and combined to give a measure of "total pigment". This procedure provides an index of total accumulated algal material regardless of its physiological condition and was considered to be a more appropriate estimator than chlorophyll *a* alone (Hawkins *et al.* 1982). Pigment concentration was also preferred to organic carbon or dry weight values since the communities that developed on plankton netting, particularly at the forested sites, included variable amounts of very fine particulate organic matter of non-algal origin.

Small pieces of netting (1.65 cm²) cut from one control and one nutrient enriched substrate per site before pigment extraction were used to examine algal community structure by scanning electron microscopy (SEM) (Rounick & Winterbourn 1983). The composition of stone scrapings (five stones per site per date) was also examined by light microscopy for comparison with diffusion-

substrate communities.

NUTRIENT-GRAZER INTERACTION EXPERIMENTS

The combined effects of nutrient additions and grazing were investigated at the Cass Spring site using diffusion substrata placed on and raised above the stream bed. Substrata were 5 cm diameter petri dishes filled with a sand-agar mixture as described by Pringle & Bowers (1984). Nutrients were added as shown in Table 2. Six petri dishes were glued to red brick tiles (one tile per treatment) and a glass-fibre filter was clamped to the diffusion surface of one dish per tile. Tiles were placed on the stream bed in a line at right angles to the current, and a second set was held 25-30 cm above the bed on a stand similar to that described by Lamberti & Resh (1983). Raising the tiles limited access to invertebrates, in particular the abundant gastropod, *Potamopyrgus antipodarum*. A potential difficulty with this protocol is that raising tiles could alter the micro-hydraulic environment. However, in both Cass and Slip Springs, releases of the dye Rhodamine-B indicated that flow over all sets of tiles was hydraulically smooth (Davis & Barmuta 1989) and that current velocities were not obviously different.

Trials set up in September 1986, October 1986, and August 1987, were run for 34, 36 and 30 days, respectively. At the end of each trial, all animals were removed from dishes and counted, and the petri dish contents were transferred to jars containing 25 ml of 90% acetone for extraction of pigments. Pieces of the glass-fibre filters were cut out and prepared for SEM viewing as described above.

GRAZER EXCLUSION EXPERIMENTS

Colonization trials were undertaken at Slip Spring on three occasions in the presence and absence of grazers. In each trial, ten large, unglazed tiles (30.2 cm^2) and a variable number of smaller ones (5.8 cm^2) were glued to each of two plastic trays that were anchored to the bed with metal pegs. One tray was accessible to grazers (principally *P. antipodarum*) but snails were excluded from the second tray, which was raised 19 cm above the substratum. Trials were run in March, April and November 1988 and ran for 14, 14 and 13 days, respectively. At the end of a trial, numbers of snails on trays were counted and "total pigment" concentration was measured as described above. The epilithon present on some small tiles was examined with the SEM.

GRAZER ENCLOSURE EXPERIMENTS

Because differences in algal biomass observed in grazer exclusion experiments could have resulted from minor differences in the light and water velocity regimes to which raised and benthic tiles were exposed, enclosure experiments with and without snails were carried out with all substrata in the same depth of water.

Flow-through enclosures similar to those described by Lamberti *et al.* (1987) were constructed from 660 ml plastic tubs with 15 cm^2 "windows" cut from opposing sides and covered with 1 mm mesh. Tubs were pressed into holes cut in a sheet of polystyrene which floated on the water surface, moored to a stake. The mesh-covered windows projected below the polystyrene raft so that the lower 3 cm of each tub was submerged and water covered the single, unglazed tile placed inside. In the first experiment at Cass Spring (March-April 1988) clean tiles and tiles pre-colonized by epilithon (3 months on a snail exclusion platform) were used in parallel trials of 28 days duration. In a subsequent 14 day experiment at Slip Spring (May 1988) only pre-colonized (2 weeks) tiles were used. In each trial, 30 (Cass Spring) or 40 (Slip Spring) *P. antipodarum* (shell height 3-6 mm) were placed in five tubs, and five remained empty. Snail densities approximated those found on stony substrata at each site. At the end of an experiment, snails were recounted and total pigment concentration on tiles was determined as described above.

RESULTS

RESPONSE OF ALGAE TO NUTRIENT ENRICHMENT

Algal biomass ("total pigment" concentration) on nutrient-enriched and control substrata at the 6 sites is shown in Fig. 1. Biomass increased with time, and except in Slip Stream was highest in Week 6 on nutrient-enriched substrata. In contrast, algal biomass was highest after 4 weeks on control substrata except at the most shaded site (Reservoir Bush Stream) where it was always very low but highest in Week 6.

Mean maximum biomass attained at forested and grassland sites ranged from 0.33 to $1.59 \mu\text{g pigment.cm}^{-2}$ and $1.95\text{--}4.44 \mu\text{g.cm}^{-2}$, respectively. Growth of algal assemblages was nutrient-limited at five of the six sites (Fig. 2), but light-limited in Reservoir Bush Stream.

Scanning electron microscopy also indicated that periphyton was denser at open than forested sites. Algal assemblages at the former were dominated by species of *Cymbella*, *Diatoma* and *Fragilaria*, whereas *Achnanthes*, *Cocconeis* and *Gomphonema* were most abundant at forested sites. Species of *Synedra* were common at all sites. The same diatoms were most abundant in stone scrapings from the respective stream types, but filamentous algae (mainly *Microspora*, *Spirogyra*, *Ulothrix* and *Zygnema*) and Cyanophyta (mainly *Lyngbya*, *Oscillatoria* and *Spirulina*) were observed more frequently in stone scrapings than on diffusion substrata.

NUTRIENT-GRAZER INTERACTION EXPERIMENTS

In all three trials at Cass Spring the periphyton that developed on grazed and ungrazed diffusion substrata was dominated by filaments of *Diatoma hiemale* var. *mesodon*. *Achnanthes lanceolata* was the most abundant understory species whereas *Synedra ulna*, two *Fragilaria* species and a coccoid cyanophyte were common but more patchily distributed.

Algal biomass (Fig. 3) was significantly higher (U-test, $P < 0.05$) on raised N+P-enriched than on control substrata in trials 2 and 3 (the N+P treatment was lost in trial 1), but the addition of nitrogen or phosphorus alone did not result in significant differences from the controls. On substrata susceptible to continual grazing one might expect algal biomass to be lower than where graz-

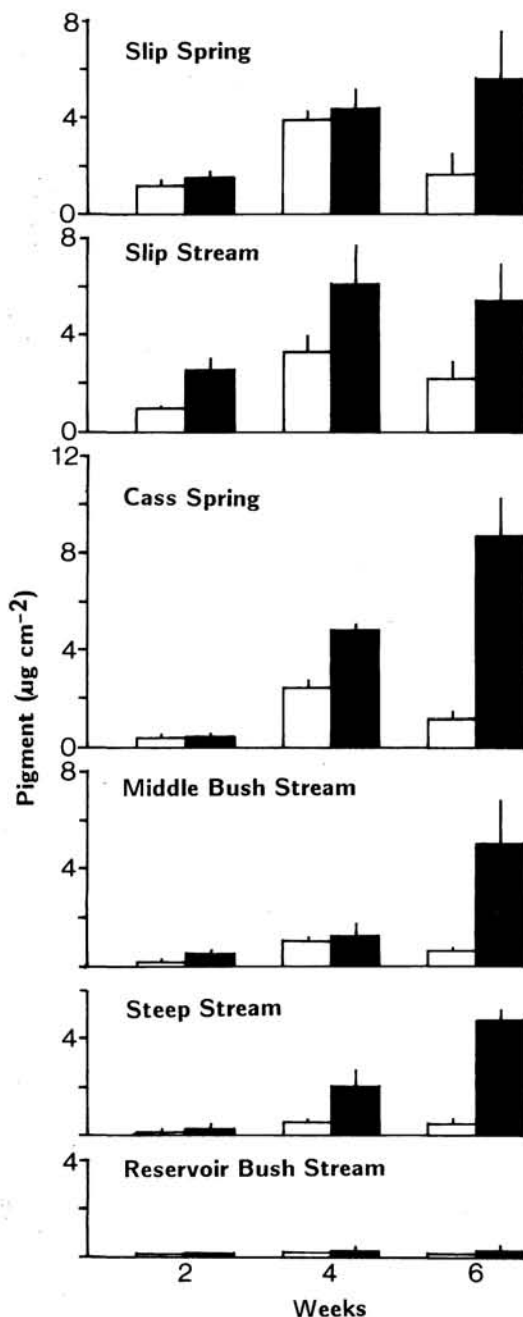


Figure 1. Pigment concentration (chlorophyll *a* + phaeophytin *a*; mean \pm 1 SE) on control (open bars) and nutrient-enriched (closed bars) substrata at six stream sites after 2, 4 and 6 weeks colonisation.

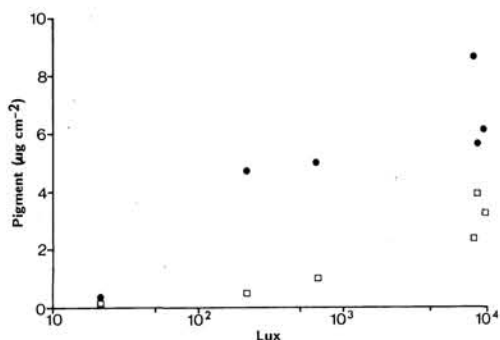


Figure 2. The relationship between maximum pigment concentration attained on nutrient-enriched (closed symbols) and control (open symbols) substrata, and mean observed illuminance at the six stream sites.

ers were absent, and also for differences between nutrient treatments to be less apparent than under ungrazed conditions. Accordingly, no significant differences (U-tests, $P > 0.05$) among grazed treatments were found in trial 3 and biomass was significantly higher on the ungrazed members of half the treatment pairs. Algal biomass was also significantly greater on the ungrazed members of three nutrient treatments in trial 2, but no significant differences were found in trial 1 when high densities of *Diatoma* were present.

GRAZER EXCLUSION EXPERIMENTS

At the end of the three exclusion trials, mean biomass of algae on tiles raised above the stream bed was 4–13 times higher than on benthic tiles (Fig. 4). No invertebrates were found on raised substrata but 34, 14 and 6 *P. antipodarum* were found on the streambed tiles (March, April and November, respectively) and we attribute the differences in periphyton standing crops primarily to their feeding activities. This conclusion is supported by SEM observations, which indicated there were marked differences in algal assemblage structure on the two series of tiles. In particular, an overstory of long *Diatoma* and *Fragilaria* filaments was abundant on raised tiles whereas *Fragilaria* was not seen on grazed tiles and *Diatoma* was represented only by short chains and single cells (Fig. 5).

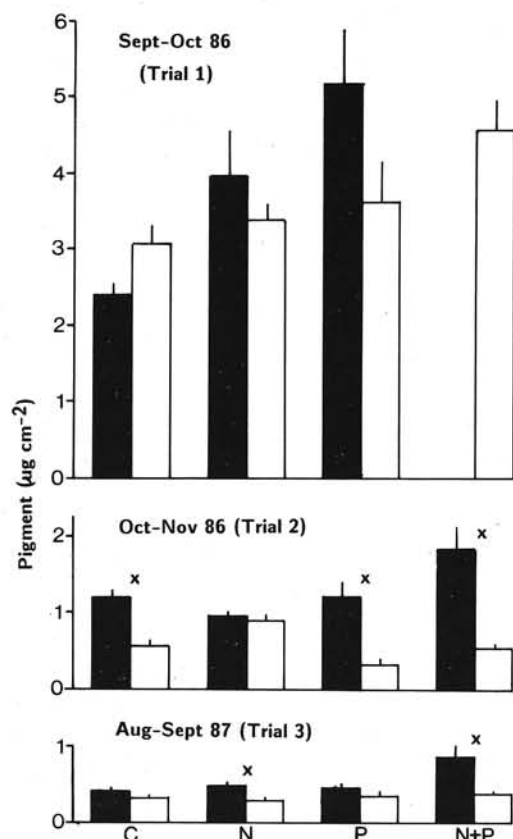


Figure 3. Pigment concentration (mean + 1 SE) on raised (closed bars) and benthic (open bars) diffusion substrata after 30-36 days in Cass Spring. C = no-nutrient controls, N = nitrogen-added, P = phosphorus-added, N+P = nitrogen and phosphorus added to substrata. x = significant differences between treatments (U-test, $P < 0.05$). Note: the raised N+P substrata were lost in trial 1.

GRAZER ENCLOSURE EXPERIMENTS

In the first experiment at Cass Spring, algal biomass on tiles exposed to grazing by 30 *P. antipodarum* for 28 days was significantly lower than on ungrazed controls (U-test, $P < 0.05$; Fig. 6). The use of clean or preconditioned tiles resulted in little difference in final biomass achieved in either treatment ($P > 0.05$), grazed : ungrazed ratios being 0.52 (initially clean tiles) and 0.63 (preconditioned tiles), respectively. In the subsequent experiment at Slip Spring, mean algal biomass on tiles kept with 40 *P. antipodarum* was 49% of that on controls after only 14 days. Experiments at

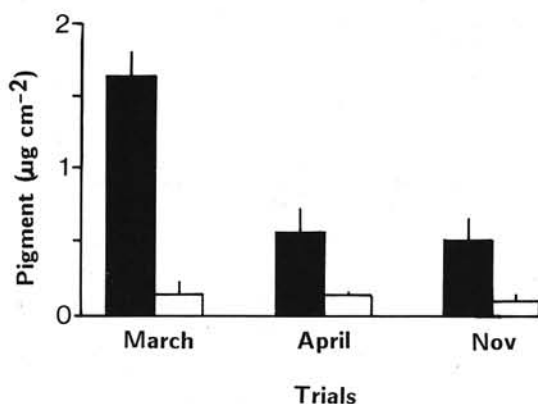


Figure 4. Pigment concentration (mean + 1 SE) on raised (closed bars) and benthic (open bars) tiles at the end of three 13-14 day trials in Slip Spring.

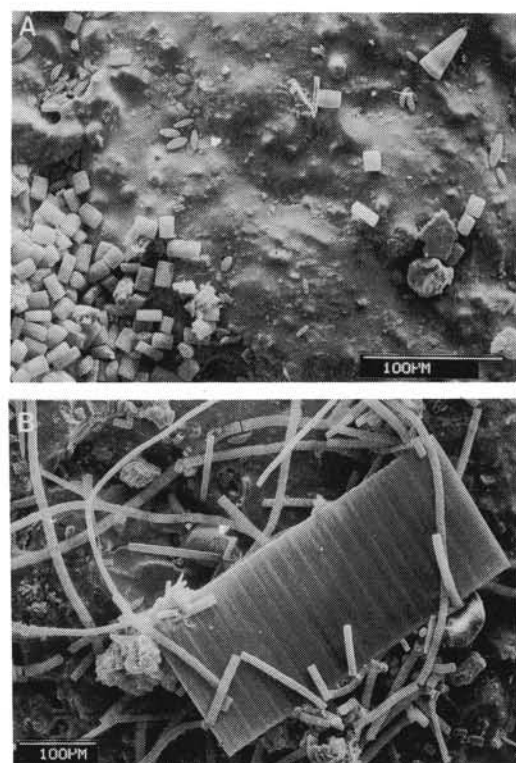


Figure 5. Typical algal assemblages on tiles after 2 weeks in Slip Spring. (a) Exposed to grazers; (b) grazers excluded. Dominant algae in (a) are individual cells and short chains of *Diatoma*, whereas in (b) long filaments of *Diatoma* and *Fragilaria* predominate.

both spring sites therefore showed clearly that at natural densities snails are capable of reducing periphyton biomass.

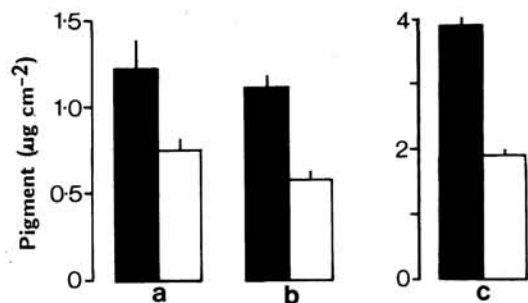


Figure 6. Pigment concentration (mean + 1 SE) on tiles held in enclosures with (open bars) and without (closed bars) *Potamopyrgus antipodarum*. (a) Cass Spring, initially clean tiles; (b) Cass Spring, preconditioned tiles; (c) Slip Spring, preconditioned tiles.

DISCUSSION

Nutrient limitation of periphytic algal growth has been documented recently in several North American studies of streams and rivers (e.g., Peterson *et al.* 1985, Grimm & Fisher 1986) and the importance of grazing as a factor influencing algal assemblage structure has been shown experimentally in the field (Lamberti & Resh 1983, Jacoby 1985, Hill & Knight 1988) and laboratory channels (Sumner & McIntyre 1982).

Our studies with nutrient-diffusion substrata also demonstrated that the growth of periphyton in both forested and grassland streams was nutrient limited, results that are consistent with those obtained in a parallel study in Middle Bush Stream (Winterbourn, in press). The latter indicated that nitrogen and phosphorus were both limiting nutrients whereas in brown water streams of South Westland nitrogen appears to be the primary limiting nutrient (Winterbourn *et al.* 1988; unpublished data). The presence of lower algal biomass in forested than open streams is usually attributed to lower light availability (Bothwell 1988). However, except in Reservoir Bush Stream, nutrients rather than light appeared to be primarily limiting at the forested sites used in the present study. Nevertheless, algal biomass achieved on control and

nutrient-enriched substrata was greater at open sites, and in part at least this appears to be a consequence of differences in the taxonomic composition of algal assemblages. Thus dominant taxa at open sites were larger, filamentous diatoms, whereas smaller, unicellular species predominated in the forested streams.

Results obtained in the experiment designed to investigate the combined effects of nutrient additions and grazing (primarily by *P. antipodarum*) were somewhat inconsistent among trials. The prevalence of *Diatoma hiemale* var. *mesodon*, with filaments of various lengths may have been a confounding factor in this experiment, but algal biomass was still higher on raised substrata than on those exposed to grazers for most nutrient treatments, and was highest on raised substrata enriched with both nitrogen and phosphorus. A grazer effect was therefore indicated by the trials and was strongly supported by the results of subsequent grazer-exclusion experiments at Slip Spring where *Diatoma* was a less conspicuous component of the periphyton. Further confirmation was provided by the enclosure experiments which showed that natural densities of *P. antipodarum* maintained algal biomass at substantially lower levels than in their absence. Grazing also resulted in the development of a structurally simpler diatom community with a lower density of erect and filamentous taxa. Such changes are consistent with those reported by Hunter (1980) and Sumner & McIntyre (1982) in experimental studies with other freshwater snails.

Many New Zealand streams provide physically harsh environments for stone-surface communities and benthic invertebrates (Winterbourn *et al.* 1981, Scrimgeour *et al.* 1988), and it is probable that frequent flooding and associated movement and abrasion of bed materials play an important role in maintaining low standing crops of epilithic algae (Winterbourn *et al.* 1988, Graesser 1989). However, the results of this study and that of Graesser (1989) in a South Westland stream, indicate that the grazing activities of invertebrates, notably *P. antipodarum* and the helicospychid caddisflies, *Rakiura vernale* and *Helicospyche* sp. can have a measurable impact on epilithic biomass.

Observations made by us in lowland, Canterbury streams and by John Quinn (Water Quality

Centre, DSIR, Hamilton; pers. comm.) in several streams receiving nutrient enrichment from oxidation ponds, also indicate that a guild of invertebrate grazers in which *P. antipodarum*, *Pycnocentroides* spp. (Trichoptera: Conoecucidae) and *Deleatidium* spp. (Ephemeroptera: Leptophlebiidae) are prominent, play an active role in maintaining a low biomass of epilithic periphyton. In order to determine the extent to which grazers play a significant role in determining the structure, production and biomass of periphytic communities in New Zealand, experimental studies will be needed in a wide range of streams and rivers.

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